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The Neural Correlates of Within Category Competition for Visual Representation

Abstract

Electroencephalography (EEG) was used to study the mechanisms of categorical perception in neurologically-normal participants. Inferring from previous studies, the N1 component of the event related potential (ERP) was explored in search of evidence of competition in the brain for visual representation. The amplitude of the N1 component may be reduced when an object is presented visually in the context of other objects of the same perceptual category. Being able to identify competition that occurs within categories of objects and not in-between objects provides a novel and powerful tool to study categorization in the intact brain. In this study, stimuli from different object categories (shoes, bonsai trees, and butterflies) were presented in the context of either objects from the same category, objects from different categories, or non-object images. The results show that there is a significant difference between the same flanker conditions and the scrambled flanker conditions which provides evidence to suggest that specific pools of neurons code for each specific categories of objects. The methods described in this study may be used in future studies to investigate categorization using competition which relieves the requirement of depending on visual agnosia patients to study competition.

Introduction

Humans unconsciously place objects encountered in the environment into categories based on their structural and functional attributes. Objects are organized based on what qualities are perceived (e.g., tool, animal, face, appliance, musical instrument, etc). By organizing different objects into different categories, our minds can give meaning to objects even if we have never encountered those particular examples before. Categorizing objects rapidly and efficiently

is thus a fundamental aspect of complex thought. The ability to give newly encountered objects meaning shows that we are able to incorporate past experiences into current and future situations without the need to duplicate the conditions in which an object was first encountered. If we were not capable of incorporating previous knowledge to new situations, our consciousness would be reduced to a cacophony of fragmented, unrelated experiences. Despite the obvious importance of categorization in the visual system, we know relatively little about how perceptual categories are organized in the brain. The goal of this current study is to improve our understanding of the mechanisms of categorization, which will shine a light into the inner workings of the human conscious experience.

Studies done on both monkeys and humans have demonstrated categorical representation of objects in the brain. Single-cell recordings in the extrastriate cortices of monkeys have revealed evidence for cells that respond to specific categories of stimuli. In one such study, Perrett and his colleagues found that 48 out of 497 neurons in the extrastriate visual cortex exhibited a greater response to faces than for other objects. These cells respond specifically to the presence of faces in the visual field (Perrett, Rolls, & Caan, 1982). The discovery of face-specific neurons responding only to faces shows us that areas of the brain involved in recognizing at least some categories of objects are quite exclusive. That is, they only represent a specific category of objects.

In humans, evidence of neurons representing specific categories includes recognizing visual words and letters. An area of the brain known as the 'Visual Word Form Area' responds specifically to these letters and words (McCandliss, Cohen, & Dehaene, 2003). Case studies of brain-damaged individuals provide evidence of specific object categorization in humans. Some of these individuals suffer from specific object agnosia, which means that they have lost the

ability to recognize a specific category of objects such as animals. Other aspects of visual perception and object recognitions in these individuals are preserved (Caramazza & Shelton, 1998). These deficits suggest that some portions of the brain are responsible for identifying that specific category of objects, and that the brain does categorize objects.

The reports of specific object agnosias, the discovery of "pools" of face-specific neurons, and the evidence that neurons respond selectively to letters or words provide strong evidence that at least some categories of stimuli are represented by anatomically discrete populations of neurons. Little evidence is available, however, as to whether these stimuli (eg faces, places, words, and letters) are somehow special such that other objects are represented in less differentiated cortical populations, or whether all object categories may be represented in their own dedicated populations of neurons. The research described in this proposal represents an effort to understand the nature of categorization in the human extrastriate cortex.

Little is known about the layout of cortical categorization. How these categories are organized is currently the topic of ongoing debate. One side of the debate argues that objects are categorized by how they are perceived functionally. The other side of the debate argues that objects that share visual features are categorized together.

Evidence that the brain categorizes objects functionally (i.e., objects with similar functions will be represented in neighboring cortical regions) comes from the previously mentioned studies on specific object agnosia. The patient from one such study could not recognize or name living things such as animals or plants, but could identify nonliving things such as tools and kitchen utensils. Another patient with similar brain damage could not identify animals, but could identify non-animal objects including plants. The loss of the ability to categorize animals and non-animals coincides with the reasoning that evolutionary pressures

have resulted in a system for conceptually distinguishing animate and inanimate objects, which leads to the categorization of that knowledge in the brain (Caramazza & Shelton, 1998).

On the other side of the debate, studies have proposed that objects that share visual features are categorized together and share similar neural substrates. That is, objects that look similar are categorized together rather than objects that share similar functionalities. The studies referred to this as the psychological distance principle. According to this principle, the more visually similar objects are to each other, the closer they are likely to be represented in cortical topography. To study this principle, Dixon and colleagues used sets of computer generated blobs as stimuli. Each set of blobs varied on certain shape dimensions such as "bendiness" or elongations. The researchers showed these blobs to a patient with specific object agnosia. This agnosia patient could not visually identify animals but could visually identify man-made objects such as tools and furniture. The agnosia was also limited to visual representations of animals, so the patient could identify sounds of animals (dog barking, lion roaring). Since real world objects cannot be elongated or bent and still look like real world objects, the study opted for an alternative approach. Instead of using pictures of real world objects, researchers asked the patient to pair the blobs with sounds of biological objects and man-made objects. In one set of trials, the researchers asked the patient to label blobs that varied on a shape dimension based on biological sounds. The researchers asked the patient to do the same with nonbiological sounds. The results showed that the patient performed similarly for both biological and nonbiological object labels. This contradicts the notion that items are categorized based on biological and nonbiological objects. Rather, the results favor a single object recognition system that varies based on shape similarities. This shows that one must consider that the brain may be categorizing objects based on shape dimensions and not on its functional properties (Dixon, Bub, & Arguin, 1997).

These two contrasting studies offer two explanations on how the brain categorizes objects. The brain could either categorize objects based on functional properties, such as animate vs inanimate objects, or based on physical properties such as elongation or curviness. The brain may also use a combination of the two. However, patients with this specific object agnosia are rare. Scientists need another way to explore the underlining of categorization.

One way to study categorization without depending on object agnosia patients is through the use of electroencephalography (EEG) recordings. By recording EEG and pairing it with some sort of stimulus such as a flashing light, scientists can measure event-related potentials (ERP). ERPs are any measured EEG response that is directly the result of a thought or perception. Recordings of EEGs show positive and negative voltage deflections in the ERP waveform at specific time points after the display of a stimulus (Mangun, Hillyard, & Luck, 1993). The amplitude of one of these deflections, known as the N1 peak or the first negative deflection is influenced by selective attention. That is, the N1 peak is influenced by visual discrimination. Thus, the N1 peak has been used to study a variety of attentional processes (Luck, Woodman, & Vogel, 2000).

Attention has been thought of as a sort of "mental spotlight" that illuminates or selects information in a region of visual space. Only a small portion of visual space can be attended to at any given time, because a full analysis of every object in the visual space would be impossibly complex. Neurological evidence in both monkeys and humans suggest that attention is an emergent property of competition between receptive fields. Receptive fields are properties of neurons dedicated to processing parts of our visual world. Each neuron is responsible for its own receptive field, and each neuron can only represent a single object. Since neurons are limited, objects falling within these receptive fields must compete for representation in the neuron. This

competition can be seen as a reduction of activity in the visual cortex (Desimone & Duncan, 1995).

In monkeys, researchers have found evidence for competitive interactions between neurons in the visual cortex. The monkeys in one study were trained to attend to a target stimulus and ignore another distractor stimulus. When both the target and the distractor stimuli were within the receptive field of a neuron, the response to the unattended stimulus was dramatically reduced. This reduction suggests that attending to the nonpreferred stimuli suppressed the neuronal activity related to the preferred item (Moran & Desimone, 1985).

In humans, evidence from functional magnetic resonance imaging (MRI) showed competitive interactions within the extrastriate cortex. The blood-oxygen-level of the extrastriate cortex was reduced when a target stimulus was presented along with competitors compared to the target presented alone. In other words, the stimuli competed for representation through mutual suppression that resulted in a lower level of activation in the extrastriate areas (Kastner, De Weerd, Desimone, & Ungerleider, 1998).

The suppressive effect of competition is particularly evident when processing faces. A waveform called the N170, which is evoked specifically by images of faces, shows diminished amplitude when a face image is viewed in context of other faces. One study tested whether the decrease in amplitude could be observed when centrally presented face stimuli were presented next to two peripheral face pictures. As a control, phase scrambled[i] faces were also presented peripherally with a central face. The N170 response to the central face stimulus was substantially reduced when it was presented next to peripheral face stimuli compared to the phase-scrambled faces. The reduction in amplitude was not seen when the faces were displayed with phase

scrambled faces. This reduction in amplitude of the N170 waveform offers a reliable measure of competition when faces are placed in close proximity to each other (Jacques & Rossion, 2004).

Recently, a study done in the Corballis lab showed that the reduction in the N1 amplitude, which is similar to the N170, was not limited to competition between faces, but it extended to houses and scrambled houses as well (Corballis, Starling, Hilimire, & Parks, in preperation)(Corballis, Starling, pmire, & Parks, in preparation). In a setup similar to the Jacques & Rossion study, images of faces and houses were used as competing stimuli. Phase scrambled faces and houses were used as controls. When faces were displayed centrally along with flanking houses, no indications of competition were found, meaning the N1 amplitude was similar to that evoked by images of faces presented in context of scrambled images. The study found the same result for central houses and flanking scrambled houses. However, when houses were displayed centrally along with flanking houses, competition did occur. Houses competing with each other but not with faces or scrambled houses suggest that the N1 waveform may not be limited to just faces and houses, but to other objects as well.

This study takes the idea of competing objects one step further. Categorical effects in the form of competition have already been shown to occur between faces and between houses, suggesting that there are dedicated populations of neurons responding to these two stimulus categories. Categorical effects have also been shown to occur between animate and inanimate objects based on the studies on the agnosia patients. Will these categorical effects occur between any two objects that are neither faces nor houses? This question was investigated using competition as an indicator for categorical effects. Using ERP data, competition between sets of images was measured by analyzing the modulation of the N1 waveform, which is a neurocorrelate of competition. In order to make the results more generalizable, the images for

this study were arbitrarily selected to be butterflies, shoes, and bonsai trees. If the results show that there is competition within categories of objects but not in-between and not with scrambled objects, there would be evidence to indicate that different pools of neurons code specifically for different categories of objects. Being able to study visual competition in this way could launch a whole new series of studies looking at how different objects are categorized without the need to rely on visual agnosia patients.

Methods

Subjects:

Participants were recruited from students on the Georgia Tech campus who were given course credit. All participants had normal or corrected-to-normal vision and been given written, informed consent before beginning experimentation.

Stimuli:

Images of bonsai trees, butterflies, and shoes were taken from a Google image search. The images were then converted to grayscale and the average luminance of each image was set to middle gray. The scrambled images were then generated by performing a 2-dimensional fast Fourier transform of image, randomizing the phase information, and reconstructing the images with the randomized phases. This procedure results in an image that preserves many of the low-level features of the stimulus (color, luminance, spatial frequency, orientation), but no longer has any sense of "objectness".

Procedure:

Participants were seated in a darkened, sound-attenuating booth. Experimental stimuli were presented on a 21-in. CRT monitor positioned 57 cm from the participant with viewing distance maintained through the use of a chin rest.

Stimuli were divided into 3 sets (A,B,C). Each set was divided into 4 blocks (1, 2, 3, 4). Sets A, B, and C contained central images of butterflies, bonsai trees, and shoes respectively. Each participant were be assigned one set of images (A, B, or C). Subjects were instructed to fixate at the fixation dot in the center of the monitor during the presentation of all four blocks (1, 2, 3, 4). In each trial, two same stimuli from a randomly selected block appeared peripherally (3.1 deg away from the center of the screen) on either side of a fixation point for approximately 900 ms. Approximately 600 ms (randomized between 500 and 700 ms) after the onset of the lateralized stimuli, a central stimuli from the selected set (A, B, or C) were presented for 300 ms in the center of the screen, replacing the fixation point. The central stimulus had a 10% chance of being upside down. The offset of the three stimuli was simultaneous and was followed by a blank screen with a fixation point for approximately 1400 ms (randomized between 1200 and 1600 ms). The participants were shown an X if they have not responded by this deadline. The participants were instructed to report the orientation of the target as quickly as possible while maintaining at least 85% accuracy. Responses were given using the space bar of a standard keyboard. Incorrect responses were signaled by an X displayed at the center of the screen. Participants completed 4 blocks of 48 trials each for a total of 192 trials. The order of trials was randomized within each block.

EEG recordings and analysis:

Electrophysiological data was recorded using a Biosemi ActiveTwo amplifier system (Amsterdam, Netherlands). Scalp potentials were recorded from 32 electrodes that included the standard 10/20 sites and a subset of the 10/10 system sites. Two additional electrodes were placed on the mastoids. Finally, the Active-Two system required the placement of two additional electrodes: common mode sense (CMS) and driven right leg (DRL). Electroencephalogram (EEG) was digitized at 512 Hz and was acquired with respect to the CMS electrode. Off-line, all channels were re-referenced to the algebraic average of all channels. Continuous EEG was bandpass filtered digitally from 0.1 to 30 Hz using a zero phase-shift Butterworth filter (12 dB/oct). Electrooculogram (EOG) was calculated off-line as the difference between electrodes positioned above and below the left eye and on the outer canthi of each eye for vertical (VEOG) and horizontal (HEOG), respectively. The EEG was segmented into 700-ms segments beginning 100 ms prestimulus and continuing 600 ms poststimulus. Segmented data was corrected for blinks and eye movements using the method described by Gratton, Coles, and Donchin (1983). The segments were then be baseline corrected by setting the average of the 100-ms prestimulus baseline to 0. Segments containing activity greater than ±80 mV were considered artifacts and rejected. If more than 25% of the total segments were rejected, then the participant was not included in the analysis. Additionally, participants with an overall response accuracy of less than 85% were also not included in the analysis. Grand average waveforms were formed from the subject averages in each condition.

Statistical analysis

Difference waveforms were plotted for all conditions of scrambled flanker vs each other flanker for each central category. These difference waveforms were then averaged across

all conditions to determine the time intervals and electrodes at which the "object" flanker conditions resulted in waveforms that differed from the scrambled flanker condition. We then measured the area under the curve for each condition in a 40ms time window centered on the maximum of the grand-average difference waves. This procedure was repeated for each central stimulus condition (shoes, trees, butterflies). For central shoes, the interval was 100-140ms and for butterflies and trees, 120-160ms. Electrodes selected for analysis were based on the maximum differences in the scalp distributions which were P7, P8, O1, and O2. Analysis of the ERP data was performed in two complimentary ways. First, the difference waves, in which the scrambled-flankers condition was subtracted from each other flanker type, were analyzed. The areas under the curve during the 40ms time window identified above were subjected to a repeated-measures analysis of variance (RANOVA) in which the factors were flanker condition (3 levels), electrode (2 levels: O vs P), and hemisphere (2 levels: left vs. right). Second, the original unsubtraced ERP waveforms were analyzed using the same time windows with flanker (4 levels), electrode (2 levels: O vs P) and hemisphere (2 levels: left vs. right) as factors for the RANOVA. Greenhouse-Geisser adjustments to the degrees of freedom were used for repeated measures tests involving more than one degree of freedom. Significant main effects and interactions identified during these analyses were further investigated using paired-sampled t-tests. For instance, if significant main effects for flankers were found, paired-sampled t-tests were conducted to compare the individual flanker condition. Finally, all data across all conditions were collapsed for the three central categories and compared using pairwise t-tests in order to analyze the overall differences between each flanker condition, same, different, and scrambled, where the shoes and trees categories was collapsed to form the different category.

Results

Grand average waveforms collapsed across the three central object conditions are shown in Figure 1. For the purposes of this study, we concentrated on the early negative difference that peaked around 120-130 ms. Note that this difference actually begins in advance of the N1 component. A 40 ms time window centered on the peak of this difference wave (shown in figure 1) was used for statistical analyses to assess the effect of different flankers on early visual activity. Note also that systematic effects of flanker type were also present in the 200-400 ms time window. These effects were not analyzed for this paper. The area under the curve during the 100-140ms time window for shoes and 120-160ms time window for trees and butterflies was subjected to a RANOVA with flanker type (3 levels: same, different, and scrambled), electrode, and hemisphere as factors. There was a main effect of flanker ($F(2,11)=6.443$, $MSe=1546.81$, $\varepsilon=.75$, $p<.05$). There was also a significant difference in the areas for same flankers and scrambled flankers conditions; $t(12)= 2.777$, $p = 0.017$, and same flankers and different flankers conditions; $t(12)= 2.618$, $p = 0.022$.

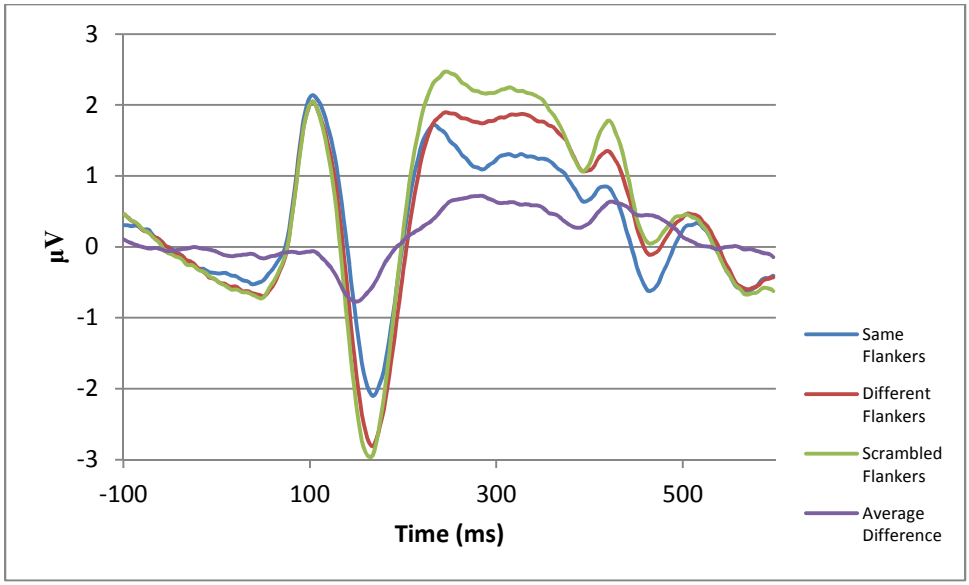

Figure 1. Average waveforms collapsed across all categories for each flanker along with the average difference waveform.

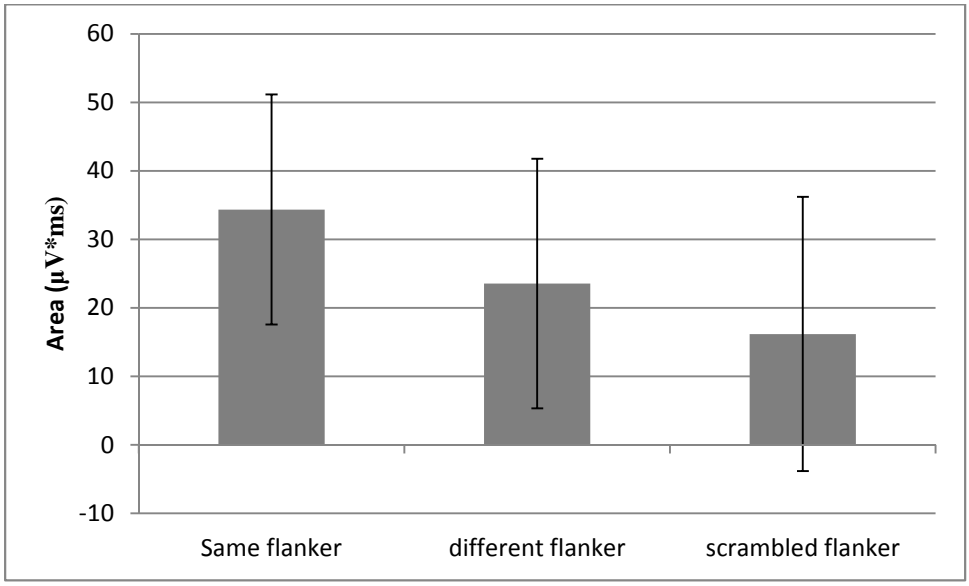

Figure 2. Average of areas collapsed over all conditions for each flanker category. Error bars represent standard error of the mean.

Analysis of Unsubstracted Waveforms

Because there were unequal numbers of subjects in each condition, separate 4 (flankers) by 2 (electrode locations) by 2 (hemispheres) RANOVAs were conducted for each central stimulus. The graphs for the unsubtracted waveforms are in the appendix.

For the ERP waveforms of the trees category, there were no significant main effects or interactions (all Fs<3.8).

In the butterflies category, there was a significant main effect of flanker ($F(3,27)=5.12$, $MSe=2006.82$, $\varepsilon=.75$, $p<.05$). There were no other significant interactions. There were

significant differences in the areas for same flanker vs. scrambled flanker; t(9)= 3.213, p = .011, areas for same vs. tree flanker conditions; t(9)= 2.389, p = .041, and areas for shoes vs. scrambled flanker conditions t(9)= 3.040, p = .014.

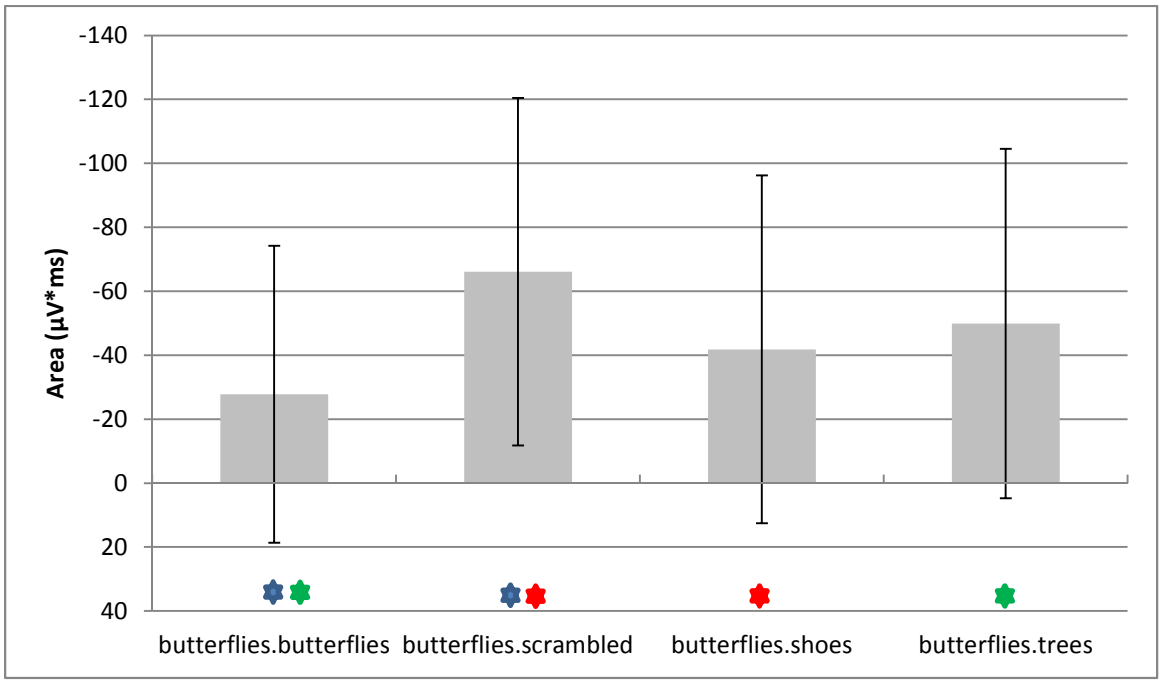

Figure 3. Average values for central butterflies vs flanker conditions. Error bars represent standard error of the mean. Note the reversed Y-axis. The paired colored stars indicate significant differences.

For the central shoes category, there was a significant main effect of flanker ($F(3,36)=4.79$, $MSe=1831.537$, $\varepsilon=.75$, $p<.05$) and a significant interaction between flanker and electrode ($F(3,36)=3.185$, $MSe=385.37$, $\varepsilon=.83$, $p<.05$). The main effect of the flanker was further investigated by collapsing across hemispheres. For the P electrodes (located over the inferior parietal lobe), there was a significant difference in the areas for same flanker vs butterflies conditions; t(12)= -2.878, p = .014, and areas for same flanker vs scrambled conditions; t(12)= 2.582, p = .024, and areas for same vs tree flanker conditions; t(12)= 3.952, p = .002 (figure 4).

For the O electrodes, there were significant differences in the areas for same vs scrambled flanker conditions t(12)= 2.489, p = .028 (figure 5).

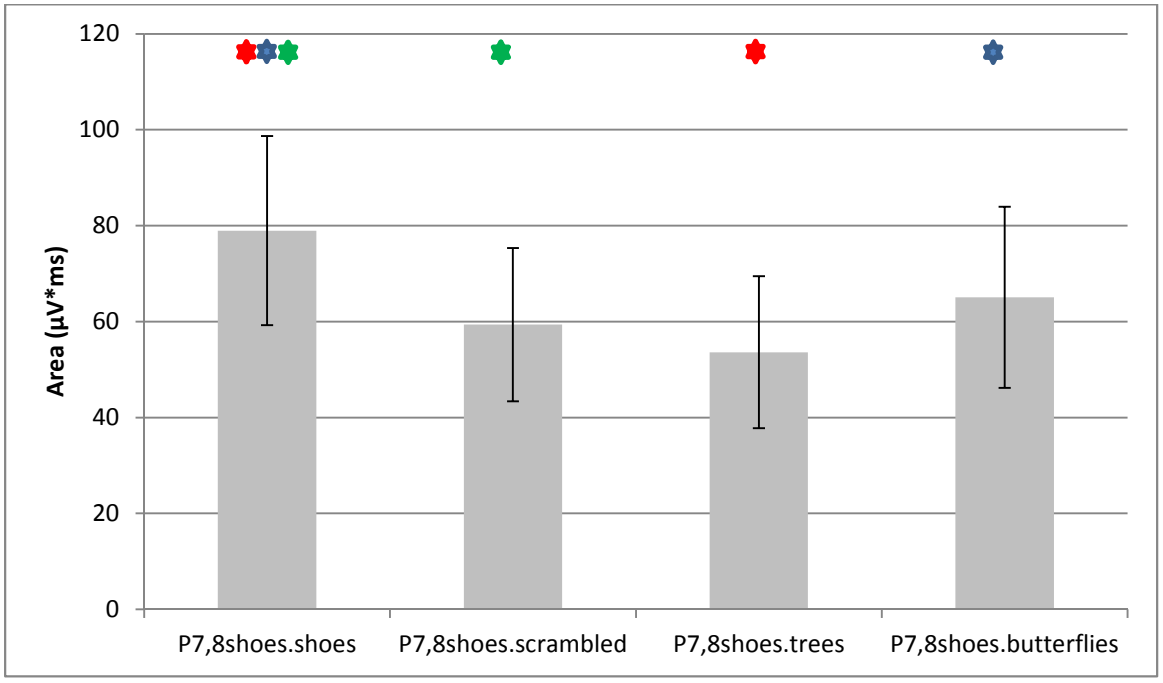

Figure 5. Mean values for P electrodes collapsed across hemisphere. Error bars represent standard error of the mean. The paired colored stars indicate significant differences.

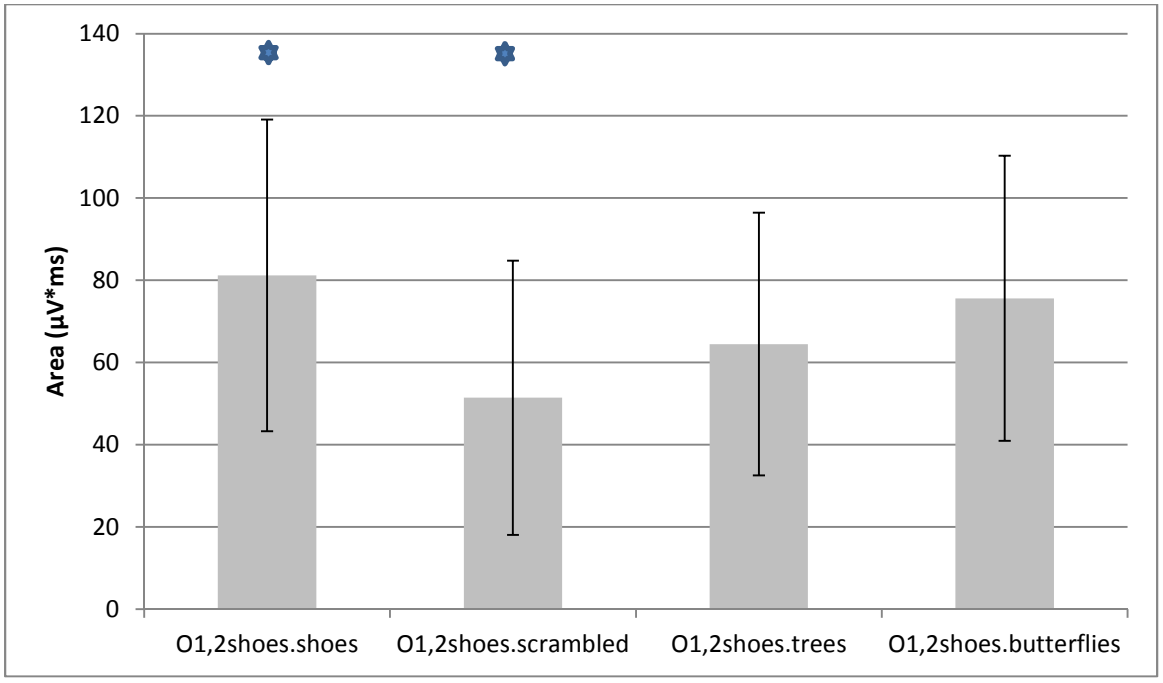

Figure 6. Mean values for P electrodes collapsed across hemisphere. Error bars represent standard error of the mean. The paired colored stars indicate significant differences.

Discussion

The results show that when collapsed over all conditions for each flanker, there was a significant difference in the areas for same flankers vs scrambled flankers conditions and same flankers vs different flankers conditions. Thus, the main conclusion that can be made from this analysis confirms our initial hypothesis: Categorical effects occur between sets of arbitrarily selected objects. More specifically, the significant differences found between the same and different categories and same and scrambled categories but not between different and scrambled categories indicate that specific pools of neurons code for each specific categories of objects. When same images are presented in context of each other, these pools of neurons compete for representation in the visual cortex whereas an image presented in context with images of other categories or non-images, competition do not occur. This extends the faces vs scrambled faces study (Jacques & Rossion, 2004) as well as the faces vs houses study (Corballis, Starling, pmire, & Parks, in preparation) which indicated similar results when analyzing the same flanker and different or non-image flankers contexts.

The objects selected for this study were chosen based on them being similar enough to be placed into a single category yet different enough to be unique within each category, which makes them good candidate images to study categorization. The arbitrary selection made the results more generalizable, meaning effects seen in this study may be replicated with any two sets of objects. Because we were able to find significant differences in the waveform between sets of arbitrarily selected sets of objects, the methods outlined in this paper could be applied to

future studies comparing other arbitrarily selected objects without relying on visual agnosia patients. An interesting question to investigate would be where the line between categories are drawn, if any. For instance, if differences can be shown between shoes and butterflies, then what about more similar objects such as shoes and sandals? Or butterflies and moths? The possible combinations are endless but nonetheless worth investigating.

For the central butterflies category, the areas calculated for the same flanker condition was significantly less than the scrambled condition indicating more competition in the same categories case which is consistent with previous literature that showed faces competing with other faces but not with scrambled faces (Jacques & Rossion, 2004) as well as houses competing with other houses but not with scrambled houses. Significant differences between the same and tree flanker conditions as well as the shoes and scrambled conditions may suggest that categorical differentiation occurs in different pools of neurons both between object categories and between object and non-object categories.

For the central shoes category, since an interaction was found between the P and O electrodes, each electrode was analyzed separately. In the P electrodes, significant differences were found between same and all 3 flanker types (butterflies, scrambled, and trees) and not between objects (trees, butterflies) or scrambled objects (object vs scrambled). Having the difference occurring for same vs everything else could mean that competition may be only occurring in same images context whereas different images may not be competing with each other. This provides additional evidence for specific pools of neurons coding for specific categories of objects. In the O electrodes, the significant difference found between scrambled and butterflies may again suggest that categorical differentiation was occurring between objects and nonobjects.

One discrepancy worth noting is the maximum average difference did not appear in the time period of the N1 as previous studies would suggest (Jacques & Rossion, 2004). Rather, the maximum difference occurred between the P1 and N1 peaks for both butterflies and shoes. This may be due to the apparent upward and right shift of the same category waveform between the P1 and the N1. This shift may also explain the greater areas for the same flanker categories of objects seen in the overall waveform as well as the shoes waveform where analysis was done at a slightly sooner interval (100-140ms). One possibility for this may be a separate pool of neurons that are not responsible for generating the P1 or N1 may be reducing the signal or there may be a new signal of decoy suppression which may be conceptually similar to the Ptc as described in another study (Hilimire, Mounts, Parks, & Corballis, 2009). The shift to the right could also indicate a slower response due to the increased competitiveness of same image stimuli. The mechanisms underlying this shift may be the subject of further research.

An important note worth mentioning for this study is the relative lack of power in each of the 3 categorical conditions with N=10,13,10 for central butterflies, shoes, and trees categories respectively. This may explain why analysis of the trees condition did reveal any main effects. There is a good chance that with more participants, more main effects, interactions, and comparisons may come to significance. All 3 categorical conditions were collapsed and each flanker was analyzed separately to increase power of the data, at expense of precision. Despite this low power, we were able to find significant differences in many of the cases, especially in the same vs scrambled categories of objects which suggest that these effects are real.

Appendix: ERP waveforms for each central stimulus condition

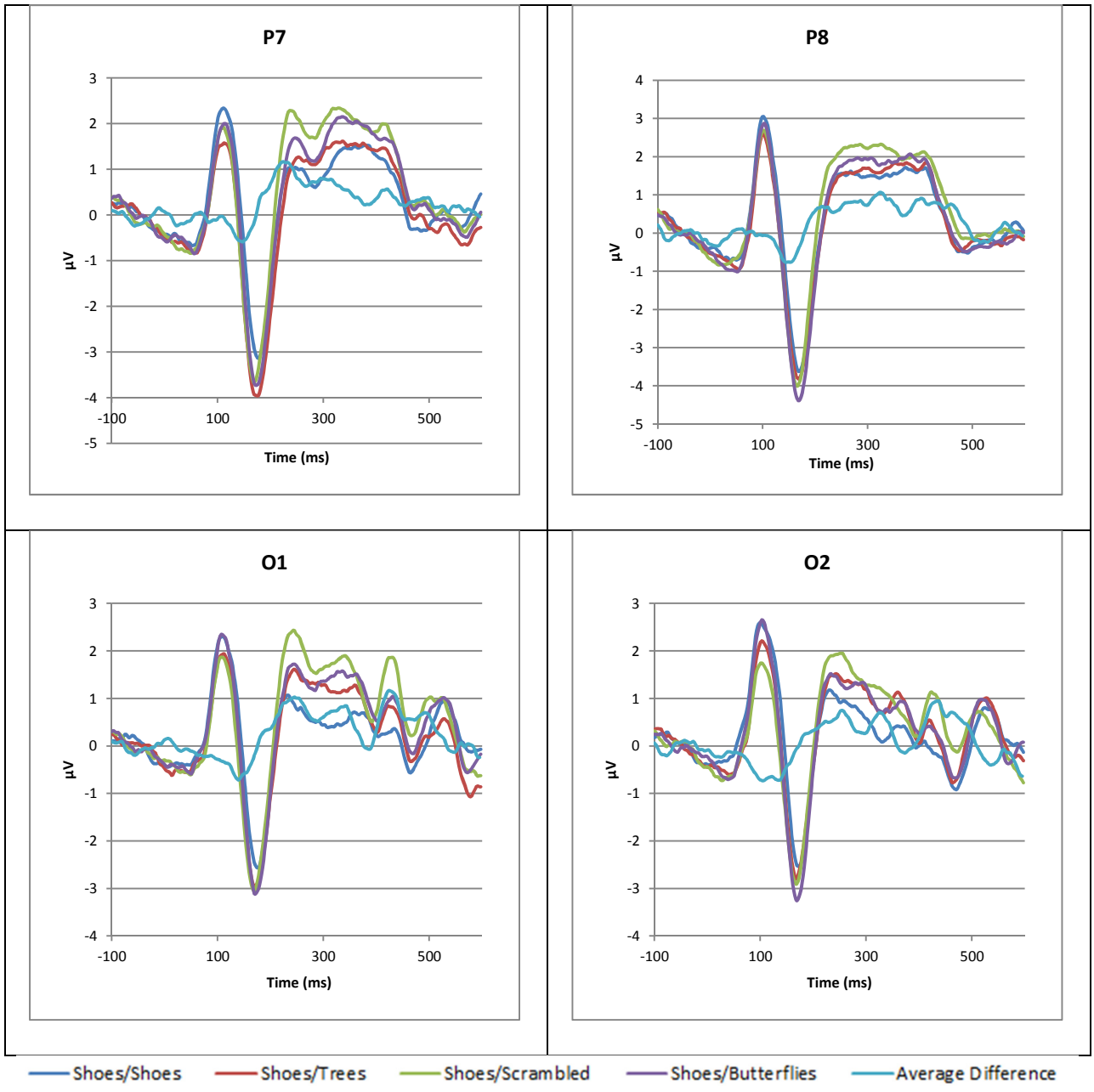

Figure 7. Average waveforms for shoes with average difference between scrambled flankers and other flanker conditions.

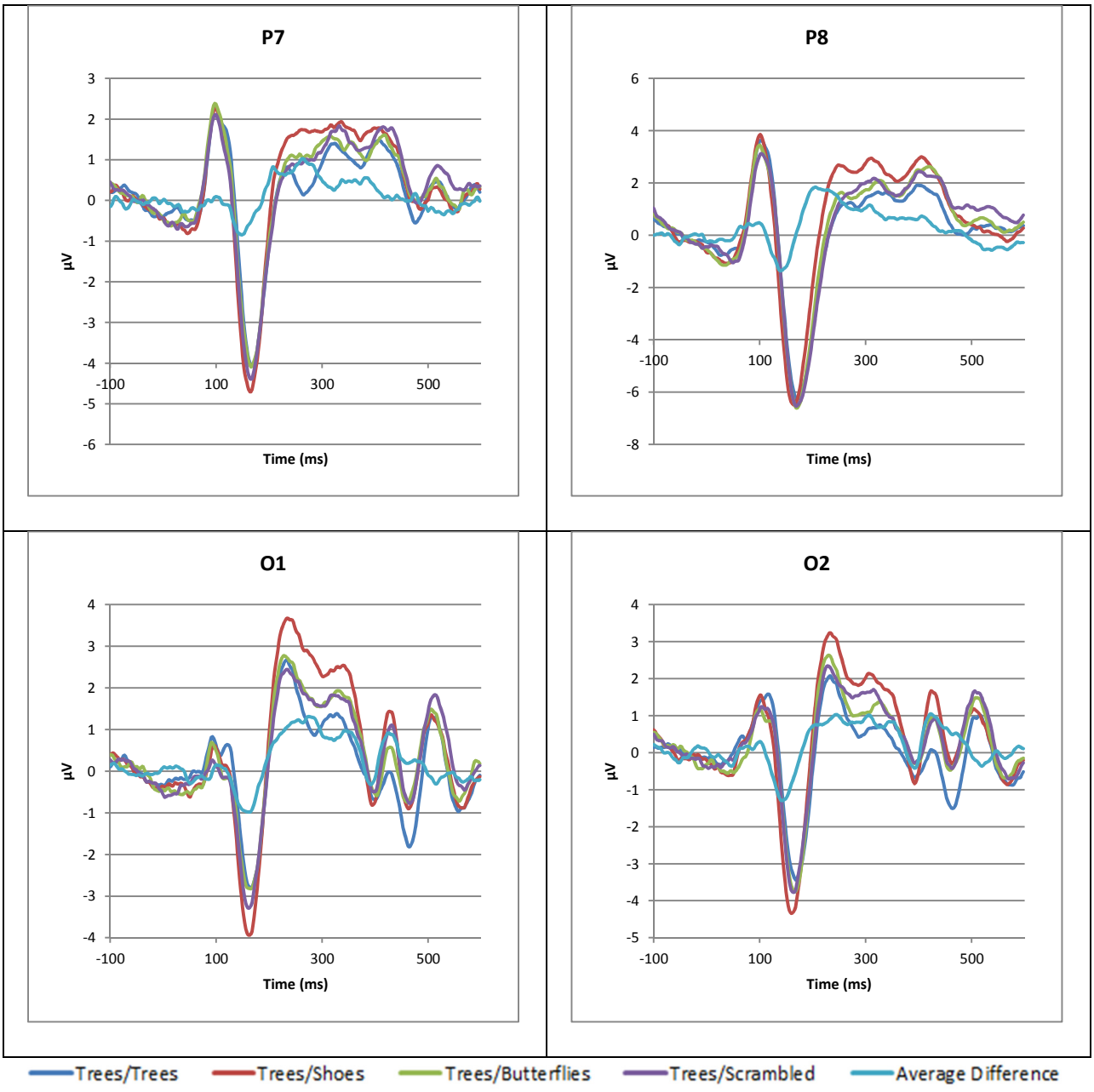

Figure 8. Average waveforms for butterflies with average difference between scrambled flankers and other flanker conditions.

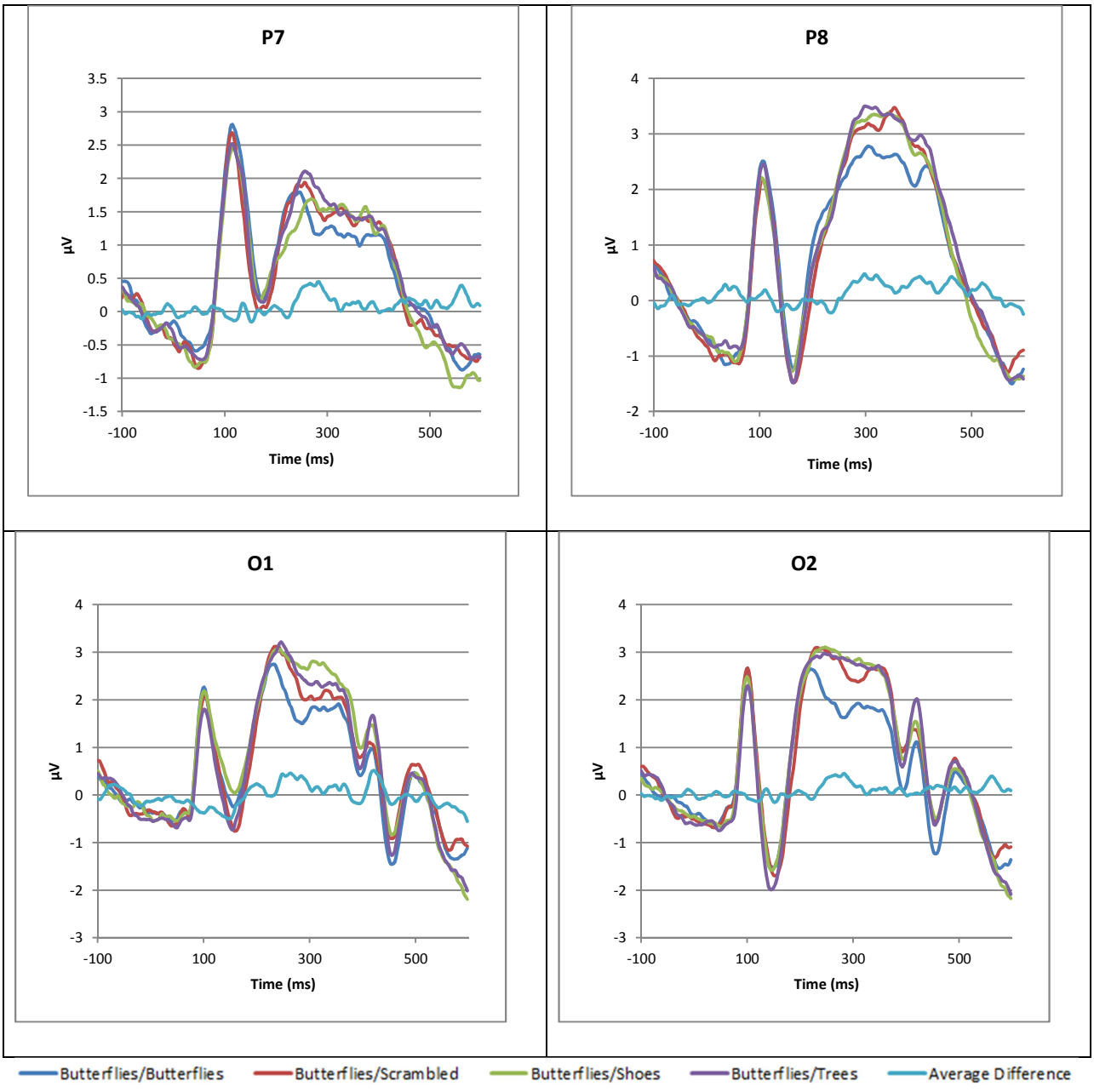

Figure 9. Average waveforms for trees with average difference between scrambled flankers and other flanker conditions.

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[i] Phase scrambling an image preserves "low level visual characteristics." These include spatial frequency, luminance, and intensity. Controlling for these variables ensures that cells in primary visual cortex were responding similarly to both the actual image and the face scrambled image. Doing so removes possible confounds and ensures differentiation only in the extrastriate cortex where the N170 is likely originating.